

## DISRUPTION, DISPERSION, AND DOMINANCE IN LEK-BREEDING BIRDS

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Recently, Bradbury (1981) provided a thoughtful review of ideas concerning lek origins as well as stimulating new hypotheses to explain the evolution of this type of social behavior. In such species, males aggregate at a site, the lek or arena, to display for females who choose among them for mates. The site contains no resources required by the females, and the males contribute nothing to the production of young except gametes. Bradbury (1981) attributed the aggregation of males on leks to the preference of females for clusters of males, a preference whose selective force overrides the opposing selective advantages to males of being dispersed. Bradbury's arguments are well reasoned and largely compelling. However, he did not consider disruptive behavior, an additional factor that I believe may significantly influence the form of the lek and the behavior of its occupants.

Disruptive behavior is any interruption of the courtship process (particularly precopulatory displays) or copulation that leads to a decrease in the number of copulations completed by a male or an increase in the amount of time and energy required to complete them. By definition, such behavior interferes with male-female interactions and is performed by a third individual (or several others). This excludes male-male disputes over dominance position or territory boundaries.

Here I will argue (1) that the frequency of disruption is proportional to the amount of contact between members of the same sex; (2) that the number of encounters is inversely proportional to the distance between males; and, therefore, (3) that the clustering of males on leks should cause increased disruption. Because disruption can be shown to be disadvantageous to males and females, I will argue further (4) that selection will operate to minimize the occurrence of disruption on the lek through the evolution of dominance hierarchies or the increased separation of males; and (5) that an equilibrium between forces favoring increased distances among males and those favoring male clustering may result in the formation of exploded leks.

## DISRUPTION BEHAVIOR

Disruption has been reported for a wide variety of lek-breeding birds, including members of the avian families Pipridae (Lill 1976; Foster 1981), Paradisaeidae (Beehler 1983), Ptilonorhynchidae (Vellenga 1970), Tetraonidae (Scott 1950; Hamerstrom and Hamerstrom 1960; Lumsden 1965; Kruijt and Hogan 1967; Wiley 1973; Robel and Ballard 1974), and Scolopacidae (Hogan-Warburg 1966; Lemnell 1978; J. P. Myers, S. G. Pruett-Jones, and F. A. Pitelka [hereafter, J. P. Myers et al.], personal communication). It is not universal, however, and its frequency varies widely both interspecifically, and intraspecifically from lek to lek or within leks, from time to time, and individual to individual. Usually, males associated with the lek are responsible, though in some species females may interfere as well (Lumsden 1968; Robel and Ballard 1974). Most commonly, disruption occurs when one male (1) supplants another at a display perch, with or without assuming his place in the courtship sequence in progress; (2) threatens the female or displaying male, causing the latter to interrupt his display to interact with the intruder; or (3) interferes with display or copulation by means of physical contact such that the activity is stopped and must be reinitiated whether the males engage in agonistic interactions or not.

Interference by females less often qualifies as disruption, as it usually involves a dominant female preventing a subordinate from gaining access to a preferred male (Scott 1942; Hamerstrom and Hamerstrom 1960; Robel and Ballard 1974). Occasionally, however, a female may interfere directly with a courting or mating pair (Scott 1950; Lumsden 1968).

## EFFECTS OF DISRUPTION ON FITNESS

Disruption behavior obviously interferes with copulation. Its effects on the fitnesses of the individuals involved, however, will depend on the identities of the disruptor and the individual whose fitness is being considered.

*Males as Disruptors*

Disruption by a male of reproductive activities at a lek may be disadvantageous for both the male and the female whose courtship he disrupts. Females of some species may avoid courts where they have experienced disruption previously (Lill 1976). A decrease in the number of copulations is obviously disadvantageous to any male, just as an increase in the energy required for successful copulation would be to either sex. In addition, an increase in the time required for successful copulation may decrease the number of females with whom a male may have the opportunity to mate; increase the amount of time a female must spend on the lek and, therefore, her vulnerability to predators (Hjorth 1968; Hartzler 1974; but see Wittenberger 1978 and Oring 1982); and in some species, affect clutch size (Bowen 1971, in Robel and Ballard 1974) and nesting success (Robel and Ballard 1974) by delaying nesting.

On the other hand, disruption may be advantageous to the interfering male if it

increases his probability of copulating. Success seems to vary among species and leks. Beehler (1983) observed three instances of disruption in the Raggiana bird of paradise (*Paradisaea raggiana*) but never saw the disrupting male copulate with the female. Lill (1976) reported that 22 (26%) of the matings he observed at a large lek of the golden-headed manakin (*Pipra erythrocephala*) were disrupted by neighboring males, although he estimated that ejaculation was actually prevented in only 7% of the encounters. At a smaller lek, the values for disruption and ejaculation were 4 (4.2%) and 0%, respectively. An additional 35% of the females visiting the large lek, and 15% of those at the small lek, were displaced from territories during courtship because of threats from disrupting males. Of the identified females disrupted at the larger lek, 50% subsequently copulated there during the same lek visit, but only 3.6% of these on the invader's territory. In contrast, 10.7% (3 of 28) of the disrupted females copulated on the invaders' territories later in the season, though these did not necessarily occur where they did because of the previous disruption. At least 10 males were involved in the disruptions, so the average advantage accruing to each was small. Nevertheless, for disruption to persist, this advantage must outweigh the costs of the disruptive behavior. Potentially, a decrease in a male's age at first reproduction could increase his lifetime reproductive output significantly (Cole 1954; Lewontin 1965).

In the buff-breasted sandpiper (*Tryngites subruficollis*) disruptor males may be more successful. J. P. Myers et al. (personal communication) reported that in 17 cases of disruption out of 38 (45%) that they observed in 1979, the female left the territory of the first male and returned with the disruptor to his territory. They did not indicate whether the females subsequently copulated with the disruptor.

Finally, in the swallow-tailed manakin (*Chiroxiphia caudata*) disruption seems to be of no benefit to the disruptor unless he is the dominant individual on the lek (Foster 1981). The males of this species have a rigid dominance hierarchy based on male-male interactions in the absence of the female. The dominant male performs all copulations in both undisturbed and disrupted sequences, though with the latter, the female may leave the court before mating occurs. Unless the disruptor is a dominant male interfering with a subordinate, he never copulates. Thus, it appears worthwhile for a bird to disrupt only if he already is the dominant individual (though subordinates do disrupt), and successful disruption in this species is really only a reassertion of rank.

#### *Females as Disruptors*

Disruption behavior by females probably represents competition among them for the opportunity to mate. Leks invariably have a surplus of males that can act as mates when females visit. Thus, all females should have the opportunity to mate with some male. However, the distribution of matings among males at a lek characteristically is highly skewed (Scott 1942; Lill 1974a; Robel and Ballard 1974; Foster 1981), so competition may exist for the opportunity to copulate with what females perceive as the better males. If a dominant female can interfere with the mating of subordinates, she may be able to mate first and benefit from advantages associated with early nesting (e.g., Robel and Blanchard 1974), or, if

she can cause her competitors to mate with inferior males, then she may be able to increase the probability that her offspring will be competitively superior to theirs. Such behaviors may be favored if a female can distinguish between kin and nonrelatives (Wilson 1975). On the other hand, Johnstone (1969, in Robel 1972) found that in black grouse (*Lyrurus tetrrix*), submissive females copulated more frequently than dominant ones. The disadvantages to the females whose copulation is prevented are the reciprocal of the advantages outlined for the disruptor.

The male whose copulations are disrupted by a female experiences the same disadvantages outlined under male disruption. Nevertheless, the fact that his copulations will be confined to more aggressive females in order of their dominance will be to his advantage if such traits among females are correlated with quality in other characteristics related to fitness. Despite this, it is unlikely that the variance in quality among females will be important. Since males do not engage in any parental care and are capable of inseminating many females, it should be to their advantage to mate with as many females as possible. This will occur, despite interference by a dominant female, if subordinate females are more likely to delay mating than to mate with nonpreferred or inferior males (Koivisto 1965; Hogan-Warburg 1966; Robel and Ballard 1974). Subordinate males will benefit from disruption to the extent that subordinate females shift to mating with them.

#### ORIGIN AND MAINTENANCE OF DISRUPTION BEHAVIOR

Although birds experiencing disruption may be placed at a disadvantage, the maintenance of this behavior by selection will depend only upon the relative fitnesses of birds that do versus those that do not disrupt when faced with courting or copulating rivals. If the only benefit to the disruptor is that he prevents another bird from breeding, then the nondisruptor benefits even more, since he incurs no cost, and the behavior should disappear. Thus, some immediate benefit must accrue to the bird that disrupts, relative to his nondisrupting counterpart, especially if such activity influences longevity or susceptibility to predators. Such behavior would be highly advantageous if, on average, the disruptor reduced his age of first reproduction and obtained more copulations as a result of his activities. This may happen in the buff-breasted sandpiper. In the swallow-tailed manakin, in contrast, copulations are increased, but apparently for the alpha male only, though if subordinates are occasionally successful, their age at first reproduction would decrease also. Additional data may show that these advantages accrue in other species as well, though in some forms, likelihood of a male engaging in disruptive behavior may be correlated with rank or reproductive success (Scott 1942; Lill 1976).

It is likely that the direct benefits of disruptive behavior are strong enough to ensure its maintenance; even so, its occurrence may be explained in another way. This behavior probably is indicative of the high levels of aggression that exist among males at a lek. Such aggressiveness presumably has been favored by selection because it is correlated in a causal way with the ability of a lek male to obtain and hold a high quality court or a high rank in a dominance hierarchy and to attract and excite females for copulation (Scott 1942, 1950; Schwartz 1945;

Koivisto 1965; Kruijt and Hogan 1967; Robel 1970, 1972; Ballard and Robel 1974; Lemnell 1978).

In black grouse, for example, females are preferentially attracted to males that fight (Kruijt and Hogan 1967; Hjorth 1970). A similar preference probably led to the evolution of communal courtship displays in long-tailed (*Chiroxiphia linearis*) and swallow-tailed manakins (Foster 1977, 1981). These displays appear to be ritualized alternate supplantings of one male by another in response to competition for a display branch. Ritualization of these displacements may have evolved as a means of conserving male energy and time. Their incorporation into the reproductive displays of the species, however, can only have occurred as a result of female choice of such interacting males.

Why females prefer interacting males is not clear, unless interaction is indicative of the relative overall quality of the males involved (Borgia 1979). If a female chooses a mate on the basis of the location of his court, and if the ability to obtain a "good" court is determined by the aggressiveness of the male, then the female's preference for a fighting male may be coincidental to her preference for the court he occupies (Lill 1974a). On the other hand, a female may examine male-male interactions, themselves, choosing a male on the basis of his demonstrated dominance or fighting ability (Alexander 1975).

Borgia (1979) argues, in contrast, that even if females prefer aggressive, interacting males, they should avoid leks or males where interaction during courtship or copulation, that is, disruption, is common, since lack of disruption should indicate a high degree of dominance of that male, relative to other males at the lek. In fact, for several species, including sharp-tailed grouse (*Pedioecetes phasianellus*) and greater prairie chickens (*Tympanuchus cupido*), amount of disruption seems to be directly correlated with instability of male-male relationships at the lek (Robel and Ballard 1974; L. W. Oring, personal communication). Females of these species may behave as Borgia (1979) suggested; when visiting the lek during the 1 to 2 wk prior to copulation, they avoid areas where male-male aggressive interactions are common (Oring 1982). Females of many other species obviously do not (Kruijt and Hogan 1967; Lemnell 1978; Foster 1981; J. P. Myers et al., personal communication).

Undoubtedly, the relative importance of the selective forces influencing disruption will vary, with the positive forces outweighing the negative ones in species that exhibit this behavior. In the swallow-tailed manakin, for example, disruption potentially decreased the number of successful copulations by ca. 20%, but the male-male precopulatory jump display, which probably evolved from the same male-male aggressive dominance encounters that led to disruptive behavior, potentially increased the number of successful copulations by ca. 40% (Foster 1981). Thus, the maintenance of this class of behavior would, on average, be favored.

#### DISRUPTION AND LEK EVOLUTION

Presumably, lek evolution is related to the lessening or elimination of female dependence upon resources controlled by the male (Bradbury 1981). As a result of this decreased dependence, the degree of female choice among males increases,

increasing the importance of sexual selection, and males emphasize self-advertisement rather than resource control. Ultimately, males do not defend a territory that includes any resources other than, perhaps, a display site.

Given this, female preference for clusters over solitary males has three obvious advantages (Bradbury 1981). First, a female can locate males easily at a cluster, especially if the cluster site is traditional; second, once at the cluster, a female can examine a large number of males quickly with relatively little traveling around; and third, clustering of males allows females to observe the choices of other females, which may be important, especially for inexperienced females, if quality of choice can be influenced by learning.

Bradbury (1981) suggested that the female preference for clusters outweighs the fact that from the males' viewpoint, selection should favor uniform dispersion of individuals. Clustering may not be advantageous to males and even may have negative effects on specific individuals if the distribution of matings among the male population is highly skewed, as seems to be the case (Lill 1974a; Robel and Ballard 1974; Foster 1981; B. Beehler, personal communication).

Disadvantages also may accrue to females as a result of their preference for male clusters. It has been shown that disruptive behavior can be disadvantageous for both males and females. I suggest that the frequency of disruption is proportional to the amount of contact between members of the same sex, and that the number of encounters is inversely proportional to the distance between males; thus, the clustering of males on leks should increase disruption. This is obvious for male-generated disruption, but applies to females as well, since by congregating at the same place to find males, females also are more apt to contact one another.

#### AMELIORATION OF DISRUPTION

Two factors seem to contribute to disruptive behavior, close proximity of individuals of the same sex, especially males, and a high level of male aggressiveness. Although each factor may influence the expression of the other, they are independent variables. Thus, selection should favor independently, mechanisms that decrease male proximity or control male-male aggressive interaction when females are present.

#### *Spacing Patterns*

Ultimately, the pattern of dispersion exhibited by males should represent an equilibrium between the opposing selective forces of female preference promoting tight male clustering, and male mating advantage (as suggested by Bradbury 1981) and decreased disruption (suggested here) promoting male dispersion. If males are too widely dispersed at a particular lek, females may prefer other leks where males are more closely grouped (fig. 1a). If males are too tightly clumped, female visits may decline because of excessive disruption. The equilibrium point will vary, with males of some species being evenly distributed through the available habitat, some clustered in "tight" leks, and others more loosely grouped on "exploded" leks (Gilliard 1963).

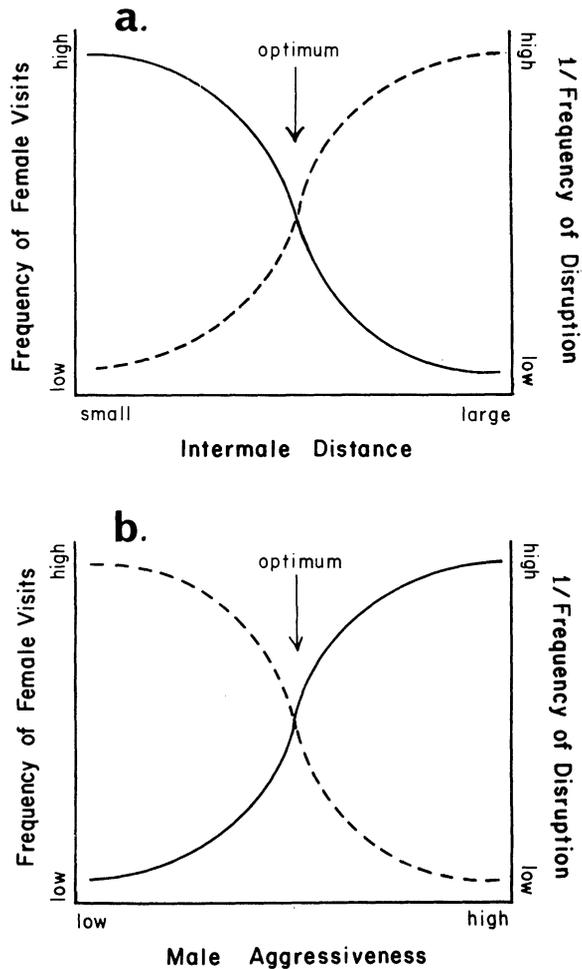


FIG. 1.—*a*, The relationships between male-male spacing and (1) frequency of female visits (solid line), and (2) frequency of disruptive behavior (dashed line). Optimal intermale distances will minimize disruption and maximize attractiveness to females that prefer clusters of males. *b*, The relationships between level of male aggressiveness and (1) ability to obtain a good court or high rank in a dominance hierarchy and to attract females (solid line), and (2) frequency of disruption behavior (dashed line). Optimal levels of aggressiveness will minimize disruption and maximize fighting ability.

Males that remain dispersed as they would be in a monogamous, territorial species may still experience disruption, but its magnitude should be less than if they were grouped. However, benefits to the females resulting from clustering will be lost. To negate completely the selective force of female preference for male clusters, disruption would have to be common and severe, a situation I suspect rarely occurs.

Another alternative is for the males to cluster loosely, forming exploded leks in which males are more widely separated than in tight leks. The size of each male's

territory or court (and thus the total area of the lek) is larger, and males often are in auditory rather than visual contact. As distance between males increases, the likelihood that one will travel to the territory of another for disruption should decrease for several reasons. First, a male may not be aware always of the arrival of a female on an adjacent territory; second, the likelihood that copulation may be completed or the female gone by the time he arrives is increased. Third, the time of his absence from his own territory will be greater, thereby increasing the likelihood that he will be absent if a female visits his area. These factors should be relatively unimportant on a tight lek where territories may be only a few meters apart.

*The nature of exploded leks.*—It is not likely that leks are positioned randomly through a habitat, but rather that they are spaced at some optimal distance relative to one another. The factors determining this distance are unknown. The observed distance between lek boundaries, which presumably reflects the optimum (fig. 2), will be determined by the density of leks in the habitat and their individual areas or active spaces (*sensu* Bradbury 1981; the area over which signals produced by males on the lek are detectable). Area of a lek (or its active space), in turn, will depend upon the number of males occupying it and the average distance between them (court size). As intermale distance, or court size, increases, as it will, for example, if tight leks give way to exploded leks as a means of countering disruption, the total area of the lek will increase. This will cause interlek distance to decrease. This can be countered, and interlek separation maintained as close to the optimum as possible, by decreasing the number of males per lek so that total lek area is unchanged (fig. 2*B*). Optimum interlek separation also can be maintained if, when lek area increases, the number of leks in the habitat decreases (fig. 2*C*).

As the density of leks increases, the number that an individual female may visit will increase. If a female contacts more than one cluster in her home range, as she probably will, she should favor one (or a few) over the rest. It is likely, in addition, that the preferences of all females in a particular area will coincide to a significant degree. Thus, some leks should consistently receive a greater number of female visits than other leks, and those consistently receiving fewer visits should gradually disappear. This would result in fewer, but larger (in area) leks (fig. 2*C*), and the number of males per lek would remain the same. Alternatively, as individual courts increased in area, the number of males per lek could decrease (fig. 2*B*) so that lek area and, therefore, number of leks, would remain unchanged. For this to occur, however, the number of males per lek at which it no longer benefits the lowest-ranking males to join or remain on a lek must decrease. This implies an inverse relationship between benefits associated with lek occupancy and size of male territory. To see how this may be so, it is necessary to consider what benefits may accrue to less successful males as a result of lek occupancy.

Foremost, of course, is opportunity to mate with a female. The probability that a marginal male on a lek will mate is very low, but will still be higher than that of a nonlek male if females confine their visits to clusters. If several females visit a lek simultaneously, as occurs in some species (Hamerstrom 1955; Lumsden 1961; Hogan-Warburg 1966; Hjorth 1970; Wiley 1973; Robel and Ballard 1974; Foster

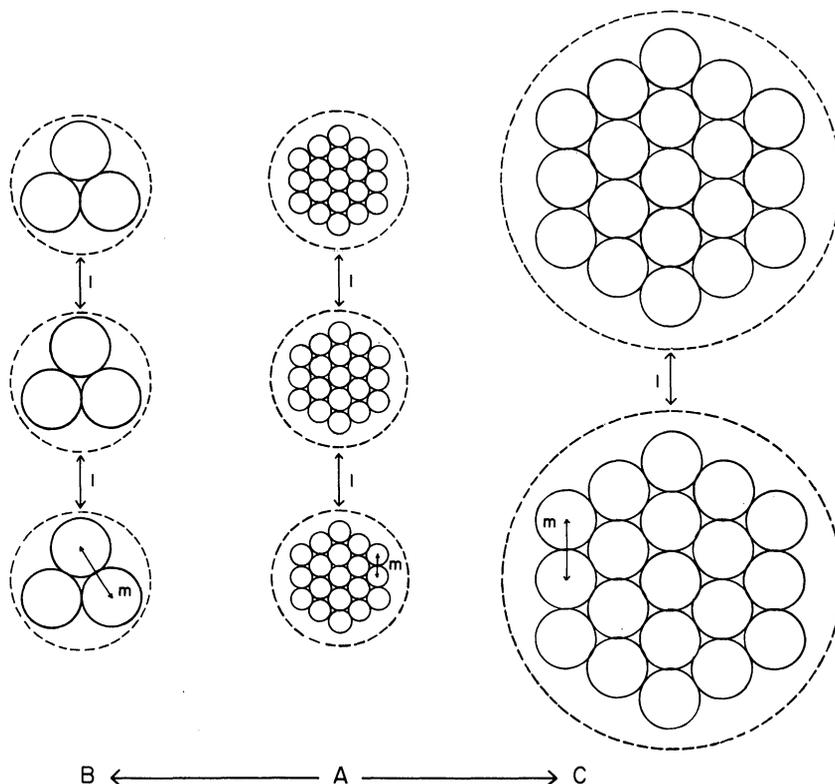


FIG. 2.—Interlek and intermale spacing. Interlek distance ( $l$ ) will be determined by the density of leks and their individual areas or active spaces (dashed circles). As diameters of male courts (small circles) increase, increasing intermale distances ( $m$ ) within the lek and transforming it from a tight lek (A) to an exploded one (B or C), either number of males per lek (B) or density of leks (C) must decrease if original interlek distances are to be maintained. Either way, fewer males will occupy leks in a given area (B or C vs. A).

1977, 1981), then less successful males may be able to copulate if the dominant males are already occupied, become satiated, or temporarily incapacitated (Scott 1942), or if access of subordinate females to the dominant male is limited by a dominant female. On the other hand, if males on the lek are widely separated, and especially if the best courts are grouped rather than randomly located, the opportunities for a marginally situated subordinate male to detect the presence of females at other courts and to attract one to his own court are greatly reduced. This is precisely the value of mechanisms that decrease disruption, benefiting the dominant male, but hurting the subordinate.

A more important benefit, perhaps, is the opportunity that less experienced, younger males may have to improve their display techniques or tactics by observing more successful males. This will affect their abilities to hold good courts and attract females in future years. To learn from a successful male, however, a marginal male must be close enough to observe him, which, on an exploded lek,

may require the marginal male to be absent from his own court. Finally, some direct benefits may accrue as a result of group living (Emlen 1978; Stallcup and Woolfenden 1978), though again, these may require some minimum proximity of group members to be operative.

Because probability of their mating is so low, combined advantages deriving from other aspects of lek association may be required to make benefits outweigh risks of lek occupancy to marginal males. If these other benefits decrease as well, as a result of male separation, then the threshold at which it is beneficial to occupy a court may be raised. This would be especially true if marginal males were young birds who by waiting a year or more could increase their ability to obtain a good court and attract females (Robel 1967).

*Predictions.*—Certain predictions that can be tested empirically follow from this discussion of lek spacing patterns: (1) Among lek species, male-male contact should be rarer in species with exploded leks than in those with tight leks. (2) The density of exploded leks will be lower than the density of tight leks (fig. 2A) for species in which the optimal distance between leks is equivalent, because each exploded lek should be larger in area (fig. 2C), or, (3) the density of exploded leks will be the same as that of tight leks for species in which optimal distances between leks are equivalent, but the average number of males per lek will be smaller (i.e., area of both types of leks will be approximately the same; fig. 2B). It is most likely that some combination of (2) and (3) will obtain. Either way, one may predict that (4) in species with exploded leks, fewer males will be involved at leks, so that the population of floating males will be larger than in species with tight leks.

#### *Tempering of Male Aggression*

If the level of male aggression is positively correlated with ability to hold a high quality court or to attract females (Scott 1942, 1950; Schwartz 1945; Kruijt and Hogan 1967; Hjorth 1970; Robel 1970, 1972; Ballard and Robel 1974), then selection will favor the maintenance of this behavior at optimal levels. The optimal level will represent an equilibrium determined by the positive aspects of aggression and its negative aspects manifest as disruption (fig. 1b). If disruption is extensive, some males may spend all their time interacting, and females may lose interest and copulate with other males (Scott 1950; Robel 1972; Foster 1981).

To counteract the negative aspects of aggression, selection also should favor, in those birds most likely to be disrupted, the evolution of behavior that will minimize disruption, whether or not male territory size or male numbers at a lek change. Selection could favor the evolution of displays that channel much of the males' aggression into ritualized behavior that may contribute to long-term, lifetime fitness by improving ability to hold good courts and to attract females. This appears to have occurred in the manakins of the genus *Chiroxiphia*, whose ritualized precopulatory displays require the participation of two males (Foster 1977, 1981).

Behavioral regulation also could be accomplished by means of a dominance hierarchy among males on a tight lek. Before this can be considered, however, it is necessary to distinguish between the two types of male aggressive behavior

commonly associated with leks. In most lek species, males interact in the absence of females to establish territories, though encounters continue throughout the breeding season as boundaries are disputed and intruders are chased. On the basis of the outcomes of these interactions, it is possible to identify dominance relationships; higher ranking males occupy the better territories and attract more females. All males with courts, however, have the opportunity to display for females, and skewness in reproductive success results from biased female choice based on direct comparison of individual males and courts at a given lek. Thus, the agonistic behavior is manifest between independent social units, the individual males, each of whom occupies an exclusive space (after Brown 1975). Such relationships are sometimes referred to as dominance hierarchies, but really represent nothing more than territorial interactions.

In true dominance hierarchies, in contrast, individuals share a space and together constitute a single social unit (Brown 1975). In these systems, hierarchies also are determined on the basis of male-male interactions in the absence of females, but in contrast to the situation outlined above, rank determines the "right" of a male to display and copulate. Thus, in the presence of a female, only one (or two) males display, and only the highest ranking male copulates. Hierarchical dominance is found among lek-breeding males of some species (Foster 1977, 1981), and is hypothesized for others (LeCroy et al. 1980).

These two types of dominance relationships probably represent the extremes of a continuum with dominance reaching its peak in the latter case in which the dominant(s) may deny subordinates the opportunity even to try to reproduce in a given area. Any degree of dominance may decrease disruption by decreasing the probability that it will be initiated, and by increasing the probability that the dominant can deal with such behavior more quickly and easily if it does occur (Lumsden 1965; Ballard and Robel 1974; Robel and Ballard 1974; Foster 1981). The more extreme the dominance, the more effective it should be in preventing disruption. Male-male activity may be slightly increased, however, if lower ranking males in a true hierarchy initiate precopulatory activity in the absence of a dominant who on his return displaces them.

Establishment of a true dominance hierarchy is equivalent to spatial "explosion" of a lek in decreasing disruption. Such true hierarchies may have evolved when less successful males clustered around more successful, dominant individuals. If the threshold for court occupancy on an exploded lek were too high, and as a result, many males did not occupy them, these individuals might find it more beneficial to become associated with a dominant male on his court than to remain as floaters. They could obtain the benefits of group living, learn by observing the dominant, and, if related to the dominant, increase their inclusive fitnesses by contributing to his success.

Such birds might be able to improve their long-term fitnesses in another way. Certain courts on most leks are more attractive to females than others, though the reasons for this are not clear. Females of some species may choose a male on the basis of quality of his court as opposed to his characteristics. Thus, even if realization of reproductive success is delayed, a male may increase his fitness by remaining subordinate at a favored court, hoping eventually to be dominant there himself, rather than by occupying a court that females rarely or never visit. This

is, in a sense, analogous to a system of delayed maturity. Here, however, a male delays reproduction until he acquires a court of some given quality rather than some physical attribute such as plumage or size. This also is reminiscent of the situation in a polygynous species in which females do better by sharing occupancy of the excellent territory of one male than they do by being the sole mate of another male with a poor territory (Verner and Willson 1966; Orians 1969). Conceivably, a male might secure more copulations as a subordinate on a good court through theft, than as a dominant on a poor court, by right.

On the other hand, a court owner might tolerate the presence of other males only if they did not display. In addition, he would have to be aggressive enough to minimize disruption by the other males in his area. If several subordinate males were present, it is likely that a hierarchy would evolve.

Although the imposition of a dominance hierarchy does not allow a female to choose among males at a particular cluster, but only among dominants at different ones, each cluster should not be considered functionally analogous to a single, sexually active male. The dominant male in a hierarchy has been tested against the other males of his group, and occupancy of the alpha position should be a measure of his "worth." Thus, the benefits that normally accrue to a female from visiting a cluster should still obtain. Single males have experienced no such tests.

#### DISCUSSION

One problem associated with testing the predictions proposed here is the precise definition of "exploded" lek. Emphasis on the presence of auditory rather than visual contact may be appropriate for forest habitats but probably will be less meaningful in open ones, especially among large birds such as grouse. An alternate criterion might be the presence or absence of contiguous territories. The capercaillie (*Tetrao urogallus*) and long-tailed manakin clearly occupy exploded leks (Lumsden 1961; Foster 1977). In both species, the areas occupied by males or male pairs are separated by zones claimed by no birds (Lumsden 1961; M. S. Foster, unpubl. data). The significant variable here is obviously the distance between males. For most species, however, designation of the intermale distance required for a lek to be called "exploded" will be arbitrary and influenced by habitat, size of the bird, and its behavior. Until more objective criteria are available, it probably is best to consider dispersion as a continuum from tightly clumped to fully dispersed individuals. Leks of similar-sized species occupying similar habitats and whose degrees of dispersion fall at different points along the continuum can be compared relative to one another. Different populations of the same species can be compared in a similar fashion.

The degree to which males must be separated in order to reduce the incidence of disruption to some tolerable level should vary among species according to the degree of female tolerance for disruption or preference for certain courts, the degree of mating skew, the type of habitat occupied, and the size of the bird. When testing hypotheses concerning lek spacing or dominance relationships, species compared should be matched for as many of these variables as possible. An alternative will be intraspecific comparison of populations showing differences in dispersion patterns or mating systems.

Male spacing or strength of a dominance relationship also will be greatly influenced by interspecific differences among males in their inherent tendencies to be aggressive and their tolerances of such behavior. In some species with tight leks, disruptive behavior is unknown or is negligible, whereas in some species occupying exploded leks, disruption is significant (B. Beehler, personal communication; J. P. Myers et al., personal communication). Unfortunately, such traits are virtually impossible to quantify.

Finally, proper evaluation of hypotheses concerning lek characteristics and origins will have to await acquisition of adequate information. In only a very few species are lek densities, court densities, and intermale relationships known, let alone size of male floater populations. Thus, many questions raised in this paper cannot be addressed at present. A few comparisons, however, are possible.

### *Pipridae*

Lek social systems are common among manakins, although only a few species have been studied extensively. Among species of the genus *Pipra*, males show varying degrees of dispersion (table 1). The number of males per lek also varies; lowest numbers occur in forms with the most widely spaced males.

Disruption has not been reported for *P. aureola*, though males visit each others' perches. Snow (1963) suggested that pairs of males may engage in joint, communal displays. A true dominance relationship could exist between them, as it does between paired males of *Chiroxiphia linearis* (Foster 1977). Males of *P. coronata* and *P. mentalis* also do not interfere with courtship activities on adjacent courts (Skutch 1949, 1969; Ridgely 1976). In *P. erythrocephala*, however, disruption of courtship and mating is common (Lill 1976). Although the data are sparse, they support the predicted relationships between male spacing and degree of disruption and number of males per lek.

Some data also are available for *Manacus manacus*, though this species may not be comparable to members of the genus *Pipra*. Here, male courts are quite close and may occur in large numbers at a lek (table 1). Disruption during courtship and mating occurs, but at an insignificant rate (Lill 1974a).

Male manakins of the genus *Chiroxiphia* are highly aggressive, as is evidenced by the form of their ritualized male-male displays (Foster 1977, 1981). *Chiroxiphia linearis* and *C. caudata* have adopted different habits that may allow them to control aggression and, thereby, decrease disruption, in different ways. In *C. linearis* pairs of males are widely dispersed on an exploded lek (Foster 1977). The incidence of disruption is very low (M. S. Foster, unpubl. data); though floating males often visit an occupied court, those with their own courts do not. In one instance, three instead of two males shared a court, and higher ranking males disrupted and displaced lower ranking individuals who displayed with females when the dominant was absent from the court. In *C. caudata*, in contrast, groups of males (4–10) occupy a lek but exhibit a linear dominance hierarchy in which only the top ranking males display or copulate (Vigil 1973; Foster 1981). Disruption is more common in this species, though it frequently involves a dominant disrupting a subordinate who initiated display in his absence (M. S. Foster, unpubl. data).

TABLE 1  
DISPERSION AND DENSITY OF MALES ON LEKS OF SELECTED SPECIES OF MANAKINS

Species	Intermale Distance (m)	Males per Lek	Disruption*	Source
<i>Pipra</i>				
<i>aureola</i> .....	30-40	2-3	--	Snow 1963
<i>coronata</i> .....	25-33	3-7	--	Skutch 1969
<i>mentalis</i> .....	6-40	3-10	--	Skutch 1949, 1969; Russell 1964; Slud 1964; Ridgely 1976
<i>erythrocephala</i> .....	1-10	2-20	++	Snow 1956, 1962 <i>b</i> ; Lill 1970, 1976; Ridgely 1976
<i>Manacus manacus</i> ...	15-2	6-70	+	Snow 1956; 1962 <i>a</i> ; Darnton 1958; Lill 1970, 1974 <i>a</i> , 1974 <i>b</i>

\* --: not reported; +: occasional; ++: occurs regularly.

#### *Tetraonidae*

Among lek-occupying tetraonids, disruption seems to be greatest in the black grouse (Kruijt and Hogan 1967; Johnstone 1969, in Robel 1972), the greater prairie chicken (Hamerstrom and Hamerstrom 1960), and the sage grouse (*Centrocercus urophasianus*) [Wiley 1973], followed by the sharp-tailed grouse (Lumsden 1961). All of these species occupy tight leks, though it is difficult to calculate the average distances between males because court sizes vary from lek to lek and within leks from place to place. Numbers of males per lek vary also. Court sizes and numbers of males for these four species are given in table 2.

The only other lek grouse for which data (table 2) are available is the capercaillie. Apparently, disruption does not occur in this species. The males occupy much larger courts than males in the other species and, therefore, on average are more widely dispersed. In addition, courts are separated by neutral boundary areas 20-50 m wide. Territories of blue grouse (*Dendragapus obscurus*), in which males are dispersed but promiscuous (Wiley 1974), are even larger (3-10 ha), and males do not interfere with reproductive activities of adjacent individuals (Hjorth 1970).

The relationship between intermale distance and degree of disruption is not as clear in grouse as it appears to be in manakins, perhaps, because the comparisons are inter- rather than intrageneric and because court sizes are so variable. If species are compared, disruption does seem to decrease when distance between males exceeds some threshold level. This holds within species as well. Wiley (1973) showed that the frequency of disruption in sage grouse depends upon the proximity of the courting or mating male to his territory boundary (i.e., adjacent males). The larger the territory the greater the area in which a male can court a female away from that boundary. The relationship between numbers of males per lek and male dispersion cannot be determined from the available data.

#### *Other Organisms*

The arguments presented have been concerned throughout with lek-breeding birds. These arguments may apply to other groups of lek-breeding organisms as

TABLE 2  
COURT SIZE AND DENSITY OF MALES ON LEKS OF SELECTED SPECIES OF GROUSE

Species	Court Size (m <sup>2</sup> )	Males per Lek	Disruption*	Source
<i>Centrocercus urophasianus</i> . . . . .	13-85	60-80† (6-400)	+	Wiley 1973
<i>Pedioecetes phasianellus</i> . . . . .	14-170 ( $\bar{x}$ = 90)	3-39	+	Ammann 1957; Evans in Hjorth 1970; Lumsden 1965
<i>Lyrurus tetrix</i> . . . . .	2-1000 (to > 4000)	3-26	+	Lack 1939; Hohn 1953; Hjorth 1963; Koivisto 1965; Kruijt and Hogan 1967
<i>Tympanuchus cupido</i> . . . . .	163-1070 (optimum = 800)	6-48 (optimum = 11-15)	+	Hamerstrom and Hamerstrom 1955; Robel 1967
<i>Tetrao urogallus</i> . . . . .	1000-8000	3-50+	- -	Lumsden 1961; Hjorth 1970

\* - - : not reported; + : occasional; + + : occurs regularly.

†Per mating center (per lek).

well, if they too exhibit disruptive behavior. Such behavior is not reported for either hammer-headed bats (*Hypsignathus monstrosus*), which occupy exploded leks (Bradbury 1977), or Uganda kob (*Adenota kob*), which occupy tight leks (Buechner 1961; Buechner and Schloeth 1965; Floody and Arnold 1975).

Wrangham (1980) may have provided an explanation for the absence of this behavior from the kob. He argued, as did Bradbury (1981), that leks arose because preference for clusters of males benefited females. One benefit, he suggested, especially for mammals, is a decrease in the amount of harassment from courting males. If this is an important factor for female mammals, then they should mate only with nonaggressive males or with males whose dominance of competitors is strong enough to prevent interference.

The absence of disruption in *Hypsignathus* may be influenced by three factors. First, males are somewhat dispersed to begin with, even during periods of maximum density (Bradbury 1977). Second, they are nocturnal, so visual monitoring of activities on adjacent territories is reduced. The third and, perhaps, most important factor may be the precopulatory behavior of the female. Females visit all males at a calling assembly at least once (Bradbury 1977). This is followed by repeated visits to two or three males over a 3–5 min period. Finally, the female chooses a mate, and copulation occurs immediately. If a male traveled to territories of other males, he would greatly increase his probability of being absent when a female visited his court. Also, by the time a male is aware that a female has chosen a mate, he may not have time to visit that court for disruption before copulation occurs.

Disruption similar to that in birds does occur in *Plathemis lydia*, a species of lek-breeding dragonfly (Campanella and Wolf 1974). In this species, courts are occupied by groups of males, group size apparently depending on court quality. When a male in the group begins to mate, the other males may interfere by means of aggressive attacks in an attempt to mate with the female themselves. On courts with small groups (1–2 males), disruption is considerably less frequent than on courts with large numbers of males (3–5), but the frequency of female visits also is smaller. Thus, females seem to prefer the latter areas despite the increased disruption which decreases their probability of mating successfully. Males within groups have true dominance hierarchies, and the alpha male (the one dominant during the optimum mating period) performs the greatest number of copulations. Campanella and Wolf (1974) hypothesized that males, by occupying good courts in groups, reduce individual expenditures for territory defense. However, differences in their aggressiveness result in the establishment of a dominance hierarchy which in turn governs access to visiting females. The dominant achieves the most copulations and the greatest reproductive efficiency through his ability to decrease chasing and interference during mating.

Male density and disruption also are related in *Drosophila grimshawi*, a lek-breeding species in which males perform communal displays that increase their attractiveness to females (Spieth 1968; Ringo 1976). When females are present, males are more apt to displace rivals physically than to display agonistically at a distance; the ratio of contact to distance aggression is correlated positively with density of males (Hodosh et al. 1979).

Dominance and disruption seem to be related in the cricket, *Amphiacusta*

*maya*, which forms tight mating groups for courtship and copulation (Boake and Capranica 1982). Males in these groups interact aggressively to form dominance hierarchies, with highest ranking males achieving the greatest mating success. During courtship, males reinforce their dominance by producing chirps (also used in male-male aggressive encounters) that discourage interruption by subordinates. Silent males experience increased interference by subordinates and, thus, reduced mating success.

#### CONCLUSIONS

The idea that disruption influences dispersion and dominance relationships of lek-breeding male birds is compatible with the variation seen in these characters among different species. Presumably, stabilizing selection, operating to maximize male reproductive success, maintains optimal levels of male aggressiveness and optimal distances between males (fig. 3). Optimal values will be expected to shift among species according to differences in degrees of female tolerance for disruption, such that males of some nonmonogamous species will be dispersed, some will be loosely clustered in exploded leks, and others will be closely grouped on tight leks.

Evaluation of these hypotheses as well as the predictions concerning the nature of exploded leks will require additional information about all lek characteristics and associated behaviors. Especially informative will be quantitative data on the success of interfering males following disruption, and the numbers and activities of floater males.

#### SUMMARY

Disruption is any behavior that interferes with male-female courtship interactions or copulation and leads to a decrease in the number of copulations completed by a male, or an increase in the time and energy required to complete them. Here I examine the origin and maintenance of disruption, its effects on the fitness of the individuals involved, and its influence on dominance relationships and spacing of males at leks. Disruptive behavior is most common among lek-breeding birds, probably because its frequency is proportional to the amount of contact between members of the same sex. Amount of contact, in turn, is inversely proportional to distance between males, so that clustering of males on leks may result in increased disruption.

Disruption usually is performed by a rival male who, as a result of his actions, may be able to mate with the female disrupted. Such behavior should be highly advantageous if, on average, the disruptor is able to decrease his age of first reproduction or to obtain more copulations. On the other hand, it is disadvantageous to the disrupted pair. Disruption also may occur as a by-product of high levels of male aggressiveness that are favored by selection because they increase the ability of a lek male to obtain and hold a high quality court or a high rank in a dominance hierarchy and to attract and excite females for copulation.

Selection should operate to minimize the amount of disruption at leks through

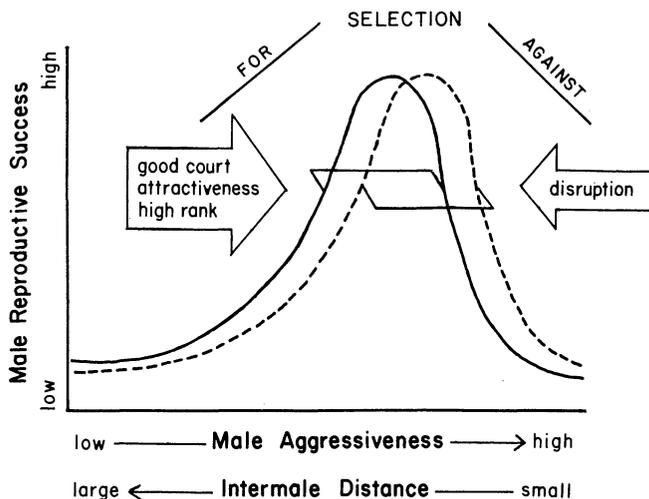


FIG. 3.—The relationships between reproductive success of males and their (1) aggressiveness, and (2) spacing. Optimal levels of aggressiveness and optimal distances between males will represent equilibria between opposing selective forces (arrows) operating to decrease disruptive behavior and to increase males' abilities to attract females and obtain good courts or high rank in dominance hierarchies. Optimal zones (in brackets) should shift to the right (dashed line) as female tolerance for disruption increases.

the evolution of strict dominance hierarchies among lek males, or by increasing the separation of lek males which may result in the formation of exploded leks.

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